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REVISION OF THE *HEDYSARUM BOREALE* COMPLEX

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INTRODUCTION

The *Hedysarum boreale* complex includes all North American members of the genus *Hedysarum* which possess free wing auricles, subequal calyx teeth, wingless loment articles, and obscure leaflet veins.

Since *H. boreale* was first described in 1818 by Thomas Nuttall, numerous variants of this taxon have been described by various authors leaving a multitude of anomalous synonyms in the literature, and the number of species described seem to greatly exceed the number of populations occurring in nature. This has made identification of members of this group of taxa, using current floristic works and monographs, quite difficult.

This revision is an attempt to ascertain and depict the pattern of morphological variation and the geographical distribution of the natural populations of the *Hedysarum boreale* complex, and then to assign a valid name to each specific or infraspecific entity.

All critical herbarium specimens examined have been cited. The herbaria from which material was made available are indicated below, and are followed by their standard abbreviations as given by Lanjouw and Stafleu (1964).

University of Alaska Herbarium, ALA; University of Arizona Herbarium, ARIZ; Brigham Young University Herbarium, BRY; University of Colorado Herbarium, COLO; University of Montana Herbarium, MONT; Montana State University Herbarium, MONTU; North Dakota State University Herbarium, NDA; Oregon State University Herbarium, OSC; Bebb Herbarium of the University of Oklahoma, OKL; Herbarium of the Philadelphia Academy of Sciences, PH; South Dakota State University Herbarium, SDU; United States Forest Service Herbarium, USFS; University of Utah Herbarium, UT; Utah State University Herbarium, UTC.

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REVIEW OF THE LITERATURE

Hedysarum boreale was first described by Thomas Nuttall in his *Genera of North American Plants* (1818). The type specimens upon which he based his description have been lost, and this, along with Nuttall's own misunderstanding of the plant, has led to numerous misconceptions concerning the identity of *H. boreale*. In his original description, which is given below (1818, p. 110). Nuttall indicated that he was not entirely sure that his plant was not *H. alpinum* of Michaux.

Caulescent, subdecumbent, leaves pinnate (7 or 8 pairs), leaflets oblong-abovate, partly villous; racemes long pedunculate, axillary, stipules sheathing, subulate; articulations of the loment nearly round, and rugose, *H. alpinum*? Mich. Fl. Am. 2. p. 74. Hab. in arid and denuded soils around Fort Mandan, on the banks of the Missouri. Flowering in June and July. Flowers of a fine red and numerous; common petiole very short; calix subulate, wings of the corolla short (*sic.*).

The description is a poor one but there are several points within it which rule out the possibility of *H. alpinum* as being the entity he was describing. Most important is the type locality, which is cited by Nuttall as "in arid and denuded soils around Fort Mandan." *H. alpinum* has not been found in that area; in fact, O. A. Stevens (1950) in his *Handbook of North Dakota Plants* does not report *H. alpinum* or any other species of *Hedysarum* except *H. boreale* for the state, leaving little doubt that the plant Nuttall described was indeed *H. boreale*. Additionally, Nuttall describes the stipules of his plant as subulate; the articles of the loment as rugose, and the calyx as subulate. These terms cannot be applied to *H. alpinum*. In *H. alpinum* the stipules are acute, the calyx teeth are triangular and the loment articles are reticulated but never rugose.

Although several workers have dealt with portions of the *H. boreale* complex, no comprehensive study has been made. Fedtschenko (1902) published a world revision of the genus *Hedysarum*, but his treatment of American plants left much to be desired. He failed to recognize the two natural groups into which the American species of *Hedysarum* fall, and subsequently he placed *H. boreale* in synonymy with *H. alpinum*. As can be seen from his specimen citations, the extent of Fedtschenko's examination of American plants can at best be described as meager.

Per Axel Rydberg (1922), in his *Flora of the Rocky Mountains and Adjacent Plains*, attempted a comprehensive treatment of *Hedysarum* but he, too, failed to recognize the two natural subdivisions of the genus. His hastily made judgments regarding species delimitation were evidently based on an inadequate number of specimens, since the characters which are truly diagnostic within the complex were not utilized in his keys or descriptions. Instead he emphasized the structure of the loments, especially the width of the internodes, the pattern of the reticulations, and the quantity of pubescence. In

addition, Rydberg seems to have been unaware of the edaphic and climatic influences on the dispersal and evolution of species, and evidently felt that it was necessary to preserve all of the taxa that had previously been described from the area.

The only significant attempt at a long-needed revision of the North American species of *Hedysarum* was that of Rollins (1940). He recognized the two natural groups into which the American species fall and correctly placed into synonymy many formerly disputable and confusing names. The paper, except for a few hastily made combinations, was precisely done, its most serious defects being its lack of experimental or cytological data, its lack of illustrations, and its exclusion of the Yukon Territory and Alaska.

DELIMITATION OF TAXA

The taxon described herein as *H. boreale* ssp. *mackenzii* has numerous synonyms, the most commonly accepted being either *H. boreale* var. *mackenzii* or *H. mackenzii*. Although an argument can be presented in favor of the application of the above ranks, the choice ultimately depends upon the definitions of the taxonomic categories involved. Although precise rank is not inherent in an entity and is determined primarily by custom, the treatment here is based upon a synthesis of the current trends in the usage of the taxonomic categories by contemporary taxonomists.

The species as it is used here may be defined as a natural population of genetically closely related individuals which are separated from other species by gaps of genetic discontinuity in morphological and physiological characters and which are maintained by the absence of gene exchange. Although a definition such as this cannot always be applied with accuracy, it is quite applicable to the North American species of *Hedysarum*. *H. alpinum*, *H. boreale*, *H. occidentale*, and *H. sulphurescens* are all separated from each other by nearly complete gaps in the assemblage of characters, and apparently little intergradation occurs between them.

One immediately realizes that because of the nature of the evolutionary process, the species may become subdivided into numerous segments, each occupying a more or less distinct area and nearly entirely confluent in morphology. A group of entities of this type is here recognized as a subspecies. They are morphologically distinct, they occupy a distinct area, and they would undoubtedly be considered as separate species by many authors, were it not for a certain degree of intergradation which they exhibit. In the following treatment, they differ not only in geographical distribution and morphology, but also in the type of habitat which they occupy. Furthermore, their areal extent is rather large in proportion to the total distributional range of the species. Although the subspecies is not popular in some circles, probably because Linneaus did not use it, it appears to be gaining acceptance due primarily to the lack of standard usage of the varietal rank.

The subspecies may be used as a hierarchical category that contains one or more small populations, herein called varieties, which are to some extent morphologically and often geographically distinctive but assume a much more localized distribution, in contrast to the commonly wide range of the subspecies. It is important to recognize that in *H. boreale* there are different levels of infraspecific variation, and thus there must be different kinds of subspecific entities. The classical rank below the level of species, the variety, is not suitable to depict all the types of infraspecific variation that occurs within *H. boreale*, and thus the hierarchical usage of both the subspecies and the variety is appropriate. At the same time, one must also recognize the limits of such a nomenclatural scheme, as too complete an analysis would result in a loss of purpose and usefulness. For this reason and because of the remarkable number of ecotypes found within *H. boreale*, no further infraspecific categories below the variety will be utilized here.

Numerous formae have been described in the past by various authors, and many times that number, each possessing at least equal stature, could be recognized. But as indicated by the tremendously wide range of variation which *H. boreale* exhibits, a recognition of all the minor forms of variation which exist in a species with as broad a distribution as this one would merely result in cumbersome keys and descriptions. To illustrate this point one needs only to examine a thorough collection of Utah specimens. Here one finds pale, pink-flowered plants in central Utah, purple-flowered plants in northeastern Utah, a large flowered phase from the foothills of northern Utah, and an extremely small flowered phase from Bryce Canyon. In addition there are populations with a tendency toward abovate leaflets, lanceolate leaflets, and compact inflorescences, as well as populations with numerous other characteristics with even less stability. In essence, the main fault with some of the previous taxonomic treatments of the *H. boreale* complex has been the failure of their authors to recognize the importance and the extent of infraspecific variation that is apparently due to ecological adaptations.

MORPHOLOGICAL CHARACTERS

Hedysarum boreale is a highly variable perennial chamaephyte, which exhibits great variation in flower size, degree of pubescence, shape and size of the leaflets, and structure of the lomenta. The abundance of synonyms herein enumerated is accounted for by the fact that much of the variation is haphazard and without taxonomic significance.

ROOTS

The root is a stout, branched, ligneous taproot, which may reach several feet in length and which is subject to little modification, except for considerable variation in length and diameter, and appears to be of no taxonomic value at this time. The roots of ssp. *mackenzii* have been reported to be poisonous, although to our knowledge this

has not been verified. Sir John Richardson, during his early expedition to the arctic (1823), evidently mistook the roots of it for those of the edible *H. alpinum* and reported that several of his men became ill after eating it.

CAUDEX

The caudex consists of from several to many stem bases which give rise to the herbaceous stems during the second and following years of growth. The nodes of the caudex branches are surrounded by thin, papery, connate, sheathing stipules. The perennating buds are found at about the level of the soil and usually give rise to a small amount of vegetative growth late in the fall before dormancy sets in.

STEMS

The stems are numerous, solid, terete, and longitudinally grooved, with the degree of branching and the length of the internodes being highly variable characters. They vary from decumbent to erect, and apparently never root along the nodes. The ssp. *mackenzii* is generally sparsely branched or even unbranched, in contrast to the often profusely branched ssp. *boreale*; but considerable variation from this pattern occurs, and thus the character cannot be regarded as diagnostic.

STIPULES

The stipules are subulate, pubescent, and usually connate, although the upper are sometimes free. The texture varies from membranaceous and white-translucent with brown streaks, to dark brown. The ssp. *mackenzii* consistently has thin, papery, white-translucent stipules while those of ssp. *boreale* may vary considerably but are usually brown.

LEAVES

The leaf of *H. boreale* is a petiolate odd-pinnate structure which bears from five to fifteen petiolulate leaflets with obscure veins, and a well defined midrib which extends to the apex. The obscure venation is diagnostic, but for some reason its significance was not recognized by the early workers.

The leaflets exhibit great variation in size, shape, and vesture; this variation is without taxonomic significance in nearly all cases. The lower leaflets are usually ovate to elliptic, although linear or obovate forms are not uncommon; whereas, the upper leaflets are usually considerably narrower and often lanceolate in shape. They vary in vesture from glabrous to canescent above and from pubescent to canescent below.

VESTURE

The herbage of all the entities within the complex are beset with some and usually many hairs. Apparently, no qualitative differences in pubescence exist. The hairs are generally from 0.5 to 1 mm in length and are straight, appressed, smooth, and silvery. They tend

to be more abundant on the upper leaves, on the inflorescence, and on the lower surfaces of the leaflets. The ssp. *mackenzii* consistently has leaflets which are green and glabrous above, and grayish green and pubescent below, whereas those of ssp. *boreale* exhibit considerably more variation but are usually pubescent on both leaflet surfaces, giving a satiny-strigose appearance; this condition reaches its extreme form in var. *cinerascens*.

INFLORESCENCE

The inflorescence is an axillary raceme which varies in the length of the peduncle and in the number of flowers. The flowers may be arranged in long, loose, interrupted racemes, as commonly occurs in ssp. *boreale*, or in subcapitulate clusters as in ssp. *mackenzii*. Each flower is subtended by a single bract which is similar to the stipules in shape and texture and tends to vary in proportion with them.

CALYX

The calyx consists of sepals connate at the base and with apices produced into five equal, subulate, pubescent teeth. The tube is campanulate, bracteolate, and is beset with usually many straight, appressed, and satiny hairs. The length of the teeth and their length in proportion to the tube have, in the past, been used to delimit taxa within this complex, but they tend to vary considerably, and thus cannot be relied upon in classification.

BRACTEOLES

The flowers of all members of the *H. boreale* complex are bracteolate. The bracteoles occur in symmetrical pairs at the base of the calyx, and appear to be of no systematic importance. The origin and significance of these appendages is obscure, but they are probably homologous with the bracts, which they tend to resemble in form.

ANDROECIUM

The stamens are diadelphous, with the filaments of nine connate into a subcylindric sheath which envelops the ovary and the remaining one free to the base. They evidently lack diagnostic significance.

GYNOECIUM

The gynoecium consists of a single elliptical and laterally flattened ovary, which contains from two to many amphitropous ovules borne on a single parietal placenta. The style is slender, curved, and glabrous, and is topped by a minute stigma.

COROLLA

The corolla of *H. boreale* is papilionaceous and consists of an adaxial banner, two free wings, and a keel opposite the banner,

which is formed from two petals coalescent by their adjacent margins, and which encloses the androecium and gynoecium. The wing petals are symmetrical and each has a blunt basal lobe (auricle) which remains free over the ovary. Except for much variation in length and width, the banner and keel are subject to little modification. Occasionally, the angle of the keel will vary somewhat, but it is of no systematic value.

The petals vary in color from nearly pure white to pink, magenta, or purple, and are often conspicuously veined. The lowermost, or oldest, flowers of the inflorescence are often considerably darker than the upper ones and tend to be somewhat larger. The ssp. *mackenzii* tends to have larger and more showy flowers than does the ssp. *boreale*.

FRUITS

The fruit of *H. boreale* is a flat loment and is constricted into several oval, indehiscent, and one-seeded articles which break transversely. The articles have transversely elongated reticulations which give a corrugated appearance, and wingless margins, although occasionally the margins are thickened. In the ssp. *mackenzii*, anthocyanin pigments are often present within the margins and reticulations of the articles, giving them a dark green or black coloration. Many previous treatments of *H. boreale* have used the structure of the loment reticulations to delimit taxa, but this character is subject to much variation both in thickness and in pattern and has no systematic value.

H. boreale var. *gremiale* has peculiar setae or spine-like structures which arise from the reticulations of the articles and are covered with hairs. These spines occasionally appear on the articles of var. *cinerascens* also, although they are never as prominent as they are in some specimens of var. *gremiale*, and may vary from minute bumps to definite tubercles.

The morphological characters that develop in a plant depend upon the environment as well as the genotype. It is evident that some genes are more sensitive to environmental fluctuations than others, and thus may have variable expressions, depending upon the particular environment in which they develop. It is quite likely that many, if not all, members of the *H. boreale* complex have the potential of developing spiny fruits, but that certain environmental conditions throughout much of the range are unsuitable for their production. The existence of intermediates with respect to the spines of var. *gremiale* strongly suggest the presence of a gene for spines which has variable expressivity, or which is modified by another gene which has variable expressivity.

The evolutionary trend in the fruit of *H. boreale* appears to be toward a reduction in the number of articles. Although ssp. *mackenzii* has a greater number of loment articles than has ssp. *boreale*, this seems quite appropriate, since it also has a much more reduced inflorescence and far fewer flowers; perhaps the greater number of loment articles compensates for the reduction in flower number.

PHYLOGENY

Hedysarum boreale ssp. *mackenzii* occurs from eastern Siberia to Newfoundland and south to British Columbia and Quebec, while ssp. *boreale* is found from British Columbia and Alberta, southward through Montana, Idaho, and North Dakota to Arizona and New Mexico (Figure 1). Where the two populations converge, plants with intermediate combinations of characters are found. These intermediates have been found from the Wallowa Mountains in Oregon, and east through southern British Columbia to central Alberta. From a close examination, it appears that a distribution such as this is best explained as a result of the extensive glaciation which is known to have occurred during the Pleistocene.

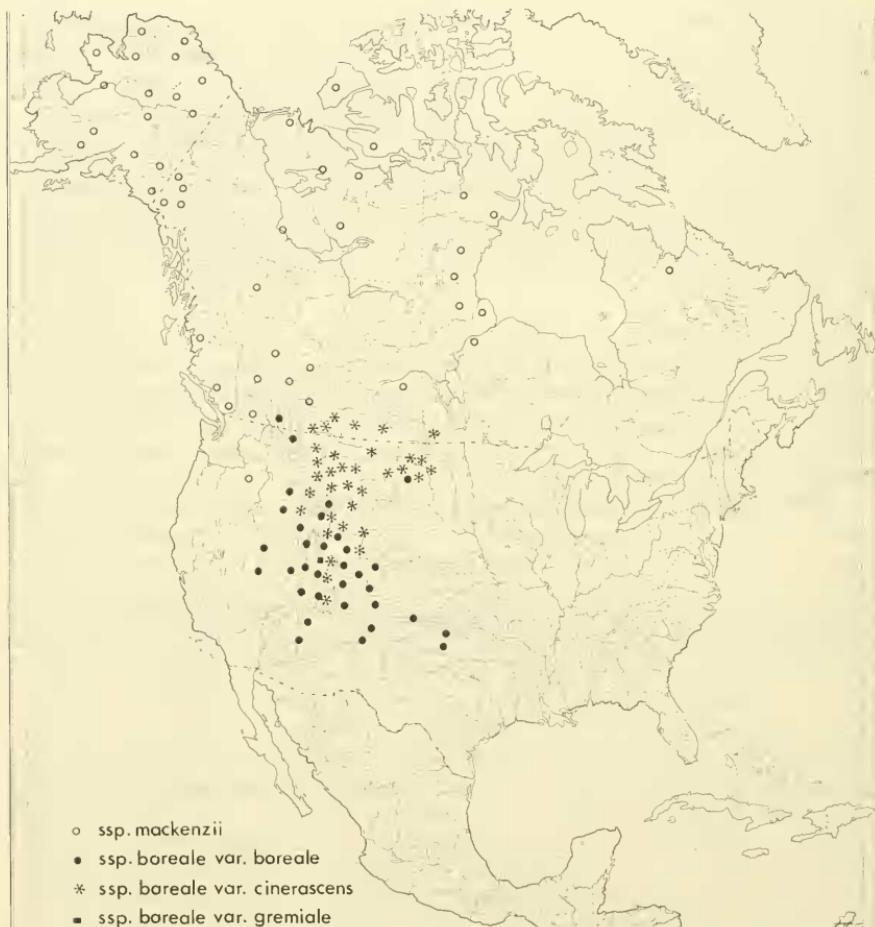


Fig. 1. Distribution of infraspecific taxa in the *Hedysarum boreale* complex.

It has been widely postulated that during the Pleistocene, because of a lack of sufficient precipitation for ice sheets to form, there were certain areas which remained unglaciated. It is thought that these unglaciated areas occupied a large part of what is now Alaska and the Yukon, portions of Quebec and Newfoundland, and numerous other smaller and more isolated areas (Hulten, 1937; Raup, 1941).

H. boreale had probably occupied most of its present range prior to the last major glaciation, but this old area became split into northern and southern segments which were separated by vast ice sheets during the Pleistocene. At the termination of the last glaciation, the species began to migrate back into its original area and eventually completely reoccupied its original range.

The segregation of the previous population into two isolated segments would tend to restrict the supply of genes available to each of these segments, and would tend to direct them into certain paths of adaptation. It is apparent that the ecological conditions found in the northern and southern areas would be vastly different from each other, and far fewer biotypes would be available for selection, especially in the north, than there were in the original area; thus, different ecotypes would be created which would later, after glaciation, give rise to major geographical races, but without the production of reproductive barriers. The initial divergence would thus be caused by the response of the ancestral population to different selection pressures, which resulted from ecological differentiation in the northern and southern portions of the original area.

It is logical to assume that the southern refugia would cover a much larger area, and the plants within it would be subjected to a wider variety of ecological conditions than would those in the north; thus, there would be more opportunity for gene flow and more phenotypic variation would be observed in the southern refugia.

It appears that this is what has occurred within the *H. boreale* complex. *H. boreale* ssp. *boreale* occupies a wide variety of habitats, and many trends of development can be observed throughout its wide range of distribution. In contrast, ssp. *mackenzii* is a pioneer and is restricted to plant communities which are in early stages of succession, especially gravel bars and areas which are flooded annually. In addition, ssp. *mackenzii* is a much more stable entity, and few trends of development are observed within it.

An attempt to explain a distribution such as this by a post glacial migration of a single species into the area, fails to account for the intermediate populations that are found in convergent areas. The only other plausible explanation would be to assume the existence of two distinct populations during preglacial times, but upon close examination of the two entities as they occur today, it is evident that the differences between them are primarily quantitative, and no truly qualitative differences exist.

The three varieties of ssp. *boreale* are differentiated either by the quantity of pubescence or by the presence of spines or hooks on the loment articles. That these characters are derived conditions in this taxon appears to be clear. Were the original population of *H. boreale*

densely pubescent, it would seem likely that densely pubescent forms would commonly occur in modern representatives of the species. But, ssp. *mackenzii* is seldom pubescent on both leaflet surfaces; furthermore, plants with dense pubescence are restricted to only a small portion of the area occupied by ssp. *boreale*.

It is also quite evident that var. *gremiale* and var. *cinerascens* are closely related. They are both usually pubescent on the upper and lower leaflet surfaces, and var. *cinerascens* commonly has definite tubercles on the loment articles. Specimens of var. *cinerascens* possessing these tubercles have been collected from Wyoming and Montana, and as far north as Alberta.

In summary, if one considers that (a) *H. boreale* ssp. *boreale* and *H. boreale* ssp. *mackenzii* are the result of the division of a pre-Pleistocene species of *Hedysarum*, and (b) that the dense pubescence of var. *cinerascens* is a derived character, and (c) that var. *gremiale* is most closely related to var. *cinerascens*, then a phylogenetic scheme can be proposed (Figure 2).

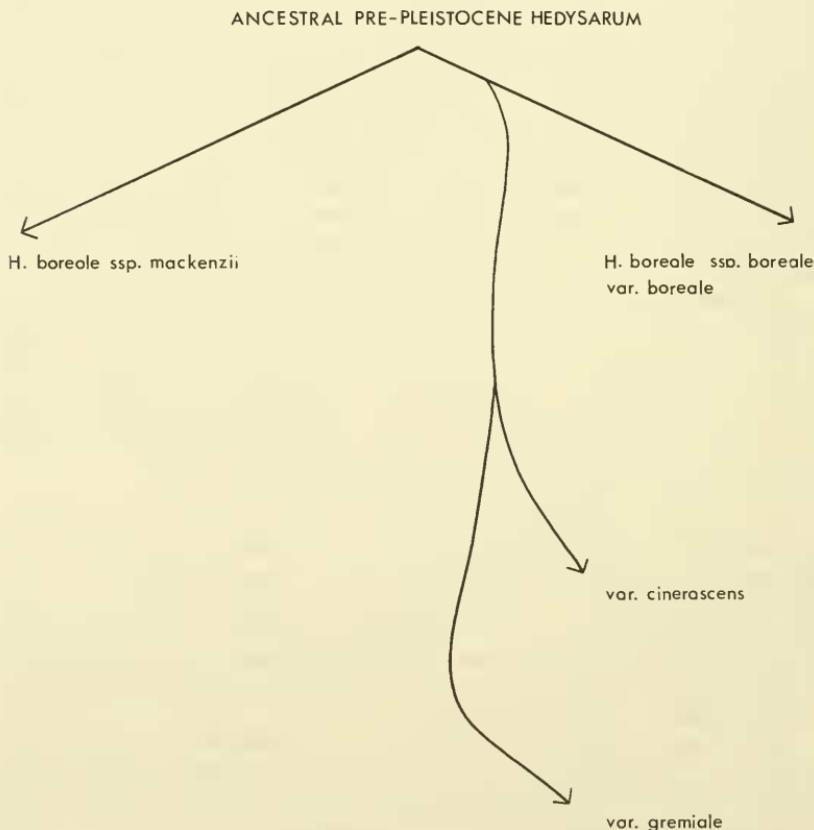


Fig. 2. Phylogenetic scheme of the *Hedysarum boreale* complex.

METHODS

When working with a species with as broad a range of distribution as *H. boreale*, the examination of an adequate number of specimens becomes especially critical. During the course of this study approximately 400 specimens were examined. The objectives of these examinations were threefold: (1) to determine the scope and frequency of variation which occurs within the complex; (2) to ascertain the geographical range, and some knowledge of the ecological requirements of the populations within the complex; and (3) to write accurate descriptions of the natural populations as they occur in nature.

All measurements of specimens were made with a standard centimeter rule graduated in millimeters. Extremely small structures were measured with the aid of a low-power binocular microscope equipped with an ocular micrometer. The flowers were measured from the base of the calyx tube to the apex of the banner or wing, whichever was longer. Since dried floral parts are subject to considerable shrinkage, all flowers were soaked in a detergent solution prior to measuring. The lomenta were measured from the point of attachment to the calyx to the apex of the terminal article.

To compare the two taxa referred to here as *H. boreale* ssp. *boreale* and *H. boreale* ssp. *mackenzii*, a tabulation on a 0, 1, 2, basis was prepared for eight morphological characters (Table 1). A

Table 1. Arbitrary values assigned to eight morphological characteristics in the two subspecies of *Hedysarum boreale*.

| | 0 | 1 | 2 |
|---------------------------------|---|--------------|--|
| Flower Color | Purple | Intermediate | Pink to magenta |
| Inflorescence | Compact 0-6 cm. | 7-12 | Elongate Greater than 12 cm. |
| Leaflets | Green and glabrous above, grayish-pubescent below. | Intermediate | Grayish and pubescent on both surfaces. |
| Stipules | White translucent, brown streaked. | Intermediate | Brown |
| Length of Flowers | Greater than 20 mm. | 17-19 mm. | Less than 16 mm. |
| Loment nodes | Narrow | Intermediate | Broad |
| Number of Loment Articles | 6-8 | 5 | 2-4 |
| Flower No. | 5-15 | 16-20 | 21-45 |

polygonal graph was then prepared (Figure 3) depicting the averages of each character for each of the two populations. It is readily observed that the width of the loment nodes, a character often utilized in previous keys and descriptions, is of little or no taxonomic value.

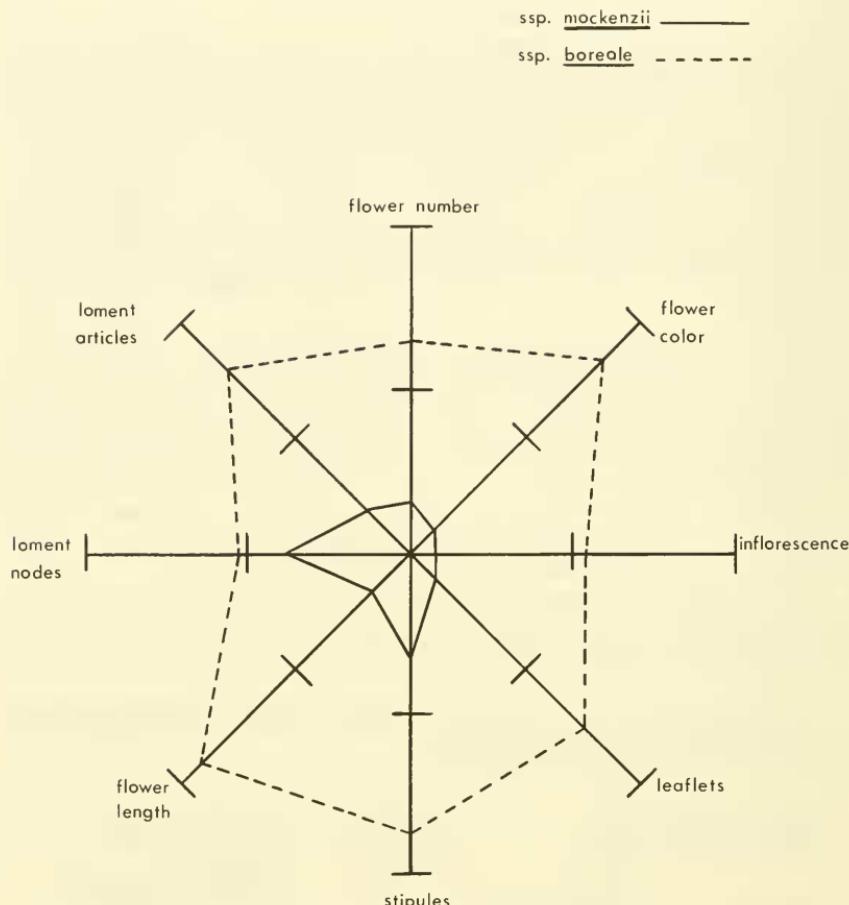


Fig. 3. Polygonal graph depicting averages for each of eight characteristics for ssp. *mackenzii* and ssp. *boreale* (based on values assigned in Table 1).

The total number of points for all characters, except those concerning the fruit, was then prepared for each specimen. The total possible range was from 0-12. The scores were then plotted in the form of a histogram which showed a distinct bimodal distribution, although some overlap between the two populations is readily apparent (Figure 4).

It is observed from the histogram that two distinct populations exist, but there is some overlap between them. Either the two races underwent complete divergence which was followed later by hybridization, or divergence was incomplete and localized swarms of intermediate individuals have been present since initial divergence began. But nearly all of the specimens with intermediate scores were found from the Wallowa Mountains of Oregon, and east to southern British Columbia and Alberta, which corresponds to the area of con-

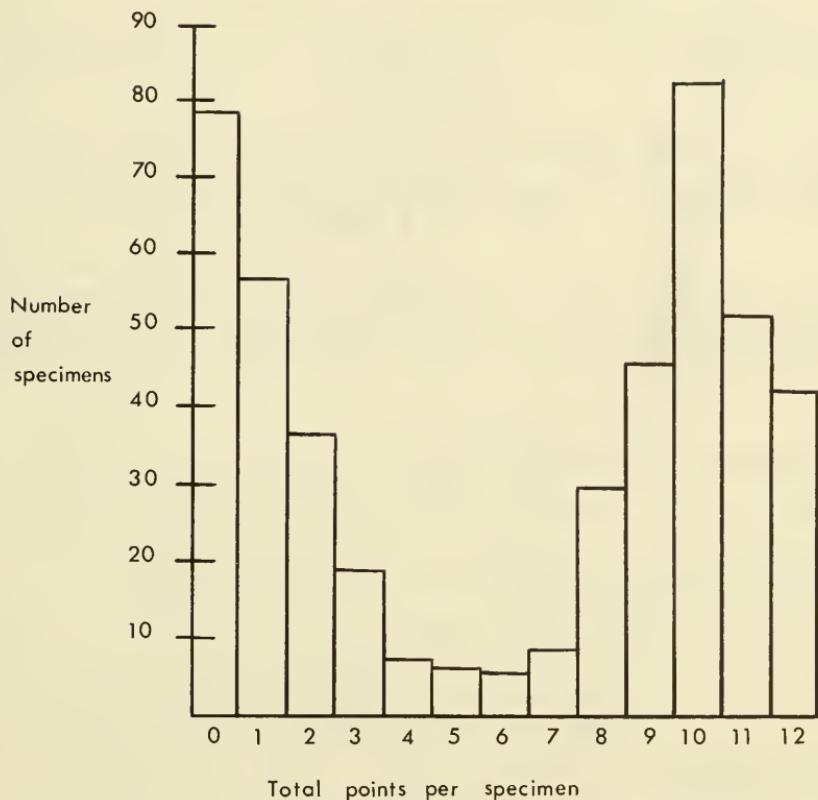


Fig. 4. Histogram based on the total points for all characteristics; 0-3 represents ssp. *mackenzii*; 8-12 represents ssp. *boreale*; 4-7 represents intermediates.

vergence of the two populations. Thus it appears that some gene flow occurs between the two entities in convergent areas (Figure 5).

CYTOTOLOGY

Somatic chromosome numbers were determined for all taxa occurring within the *H. boreale* complex. The somatic chromosome number of 16 was found in all taxa.

TAXONOMY

Hedysarum boreale Nuttall, Gen. N. Am. Pl. 2:110. 1818.

Common Name: Sweetvetch.

Terrestrial, herbaceous perennials; roots stout, ligneous, 4-12 mm in diameter; stems 2 to many, decumbent to erect, longitudinally grooved, not rooting, 2.5-7 dm long, 1.5-5 mm in diameter, usually branched above, solid, terete, sparsely pubescent to canescent; stipules tan to brown, or white-translucent with brown streaks, with a sub-

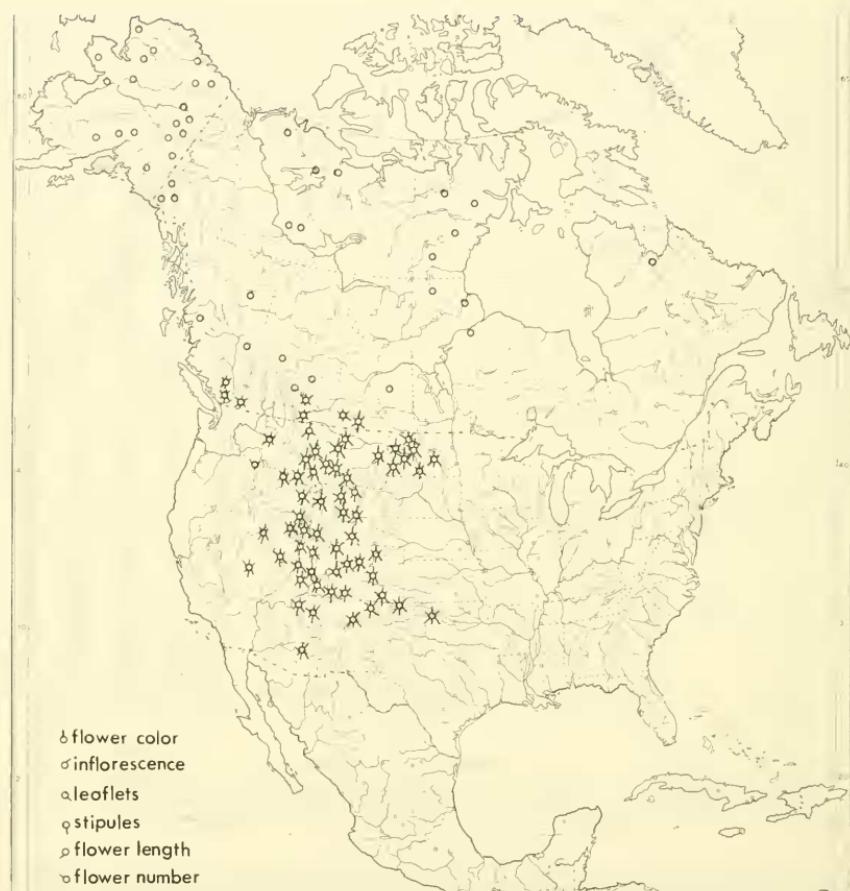


Fig. 5. Distribution of variability in *Hedysarum boreale* complex (based on values assigned in Table 1).

ulate tip, usually united, upper sometimes free, 2-10 mm long; leaves odd-pinnate, 3-12 cm long; leaflets 5-15, ovate, elliptic, linear, or obovate, canescent to glabrous above, canescent to pubescent below, entire, veins usually hidden, 10-35 mm long, 3-19 mm wide, apices rounded to obtuse; inflorescence racemose, 2-15 cm long, interrupted to compact; bracts subulate, brown, pubescent, 2-5 mm long; bractiolas pubescent, linear, 1-3 mm long; flowers 5-45, erect to spreading, pink to purple, 10-26 mm long; calyx tube campanulate, 4-8 mm long, bractiolate, pubescent, calyx teeth 0.5-1.5 mm wide, 2-5 mm long, subulate, greenish, erect; standard obovate to cuneate or spatulate, apex emarginate, base cuneate, 8-16 mm long, 4-10 mm wide; wings 6-16 mm long, 2-5 mm wide; wing auricles blunt round, free, 1-2 mm long; stamens 10, diadelphous; style slender,

curved; loments pendulous to spreading; articles 2-8, pubescent or setaceous, stipitate, not wing-margined, prominently transversely reticulated.

KEY TO THE SUBSPECIES

1. Flowers mostly 10-19 mm in length, pink to purple; racemes 8-23 cm long; articles mostly 2-5. ssp. *boreale*
1. Flowers mostly 15-26 mm in length, usually purple; racemes compact, usually 2-10 cm long; articles mostly 3-8. ssp. *mackenzii*

Hedysarum boreale Nutt. ssp. *boreale*

Stems 2.5-7 cm long, usually branched above; stipules usually pale brown, occasionally brown streaked; flowers 13-45, 10-19 mm long, pink to magenta or purple; racemes elongated, 8-23 cm long; leaflets usually pubescent on both surfaces, occasionally glabrous above; articles 2-5, seldom black-pigmented.

Key to varieties of ssp. *boreale*

1. Articles of the loment covered with spines; leaves pubescent on both surfaces or glabrous above. var. *gremiale*
1. Articles of the loment lacking spines; leaves pubescent to canescent on both surfaces or occasionally glabrous above.
 2. Leaves glabrous to sparsely pubescent on upper surface. var. *boreale*
 2. Leaves markedly pubescent on both surfaces, whole plant grayish hairy or canescent. var. *cinerascens*

Hedysarum boreale Nutt. ssp. *boreale* var. *boreale* (Fig. 6, A-D)

H. carnosulum Greene Pittmania, 3:212. 1897.

H. pubulare A. Nels., Proc. Biol. Soc. Wash. 15:185. 1902.

H. utahense Rydb., Bull. Torrey Bot. Club, 34:424. 1907.

H. pubulare var. *rivulare* Williams. Ann. Mo. Bot. Gard. 21:344. 1934.

H. mackenzii var. *pubulare* (A. Nels.) Kearney and Peebles, Journ. Wash. Acad. Sci. 29:485. 1939.

H. boreale var. *typicum* Rollins, Rhodora, 42:232. 1940.

H. boreale var. *utahense* (Rydb.) Rollins, Rhodora. 42:232. 1940.

H. mackenzii var. *fraseri* B. Boi., Canad. Field-Nat. 65:20. 1951.

DISTRIBUTION: In grasslands or on sagebrush slopes in the lowlands, to open fields or woodlands in the mountains. British Columbia to Alberta, south through Idaho, Montana, and North Dakota to Arizona and New Mexico. Also in eastern and central Nevada. It merges in the north with the ssp. *mackenzii*.

Representative specimens:

ARIZONA: Apache Co., Salakhai Mesa, *Deaver*, s.n., 7 August 1952 (ARIZ); Navajo Co., 15 mi. S.E. of Snowflake, *Hevly* s.n., 26 June 1962 (UT, ARIZ); North Base of Black Mesa, *Shreve* 8968, 21 June 1939 (ARIZ, UT, COLO).

BRITISH COLUMBIA: Yoho Park on Mt. Stephen, *Ulke* 175, 2 August 1927 (MONTU); Marble Mts., *Thompson* 195, 20 June 1938 (PH).

COLORADO: Boulder Co., North of Boulder, *Bethel* 4170, 22 July 1921 (MONTU, UTC, COLO, PH). Dolores Co., T. 39 N., R. 14 W., *Ownebey* 1477, 26 August 1937 (PH, UTC, MONT). Eagle Co., Holy Cross Forest Station, *Rice* 351, 18 July 1941 (USFS). Fremont Co., South of Canon City, *Ewan* 14225, 12 June 1942 (COLO). Las Animas Co., 20 mi. northwest of Branson, *Rollins* 1864, 14 July 1937 (UTC, USFS, MONT). Mesa Co., Colorado National Monument, *Pennell* 22144, 24 June 1938 (PH); Montezuma Co., Mesa Verde Natl. Park, *Welsh* 2082, 7 June 1963 (BRY, SDU); Switchback road below Point Lookout, *Welsh* 3029, 13 June 1964 (BRY).

IDAHO: Butte Co., National Reactor Test Station, *Atwood* 914, 8 June 1967 (BRY). Custer Co., Lost River Mts., *Hitchcock* 11109, 14 August 1944 (UTC).

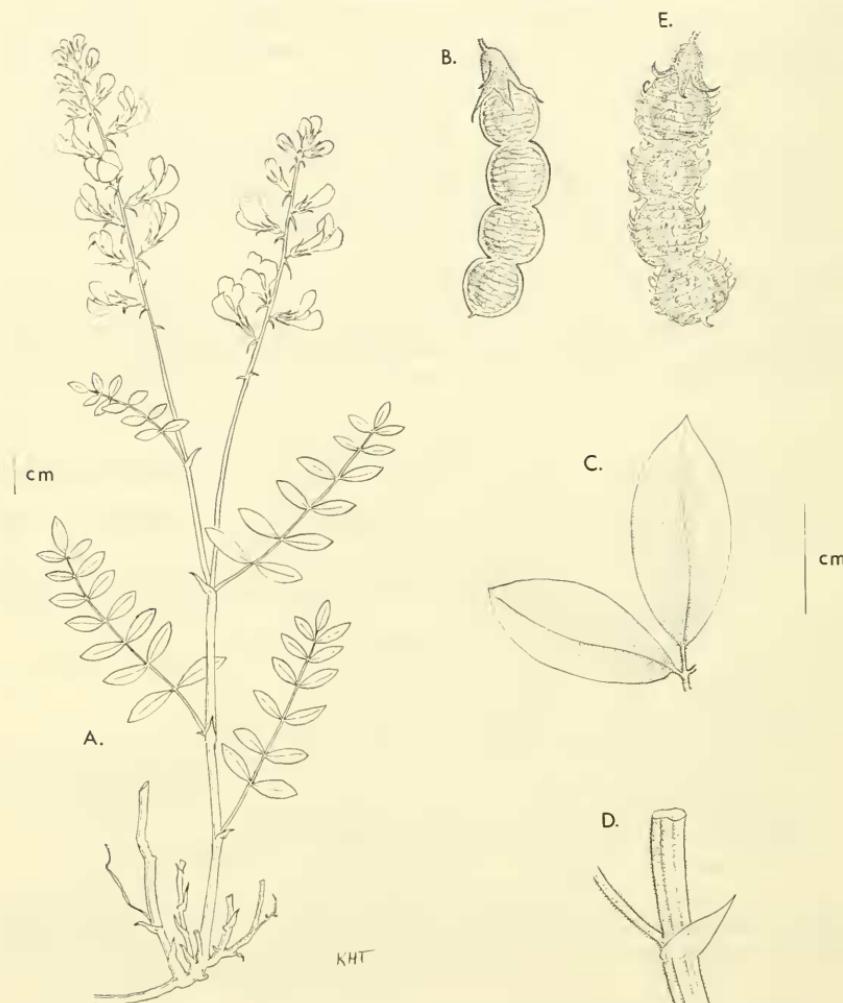


Fig. 6 *Hedysarum boreale* ssp. *boreale*: A. habit sketch. B. loment. C. leaflet detail. D. stipule detail. *Hedysarum boreale* ssp. *gremiale*: E. loment.

MONTANA: Gallatin Co., Gallatin Forest, Bear Creek, *Whitman* 1811, 31 July 1935 (USFS). Golden Valley Co., Northwest of Levina, *Booth* 55222, 26 June 1955 (MONT). Jefferson Co., *Moran* s.n. 23 June 1965 (BRY). Lewis and Clark Co., 25 mi. N. of Augusta, *Hitchcock* 18074, 6 July 1948 (UTC, COLO). NEW MEXICO: Colfax Co., East of Colfax, *Goodding* G143-40, 13 June 1940 (OSC); Raton, *St. John* 147, July 1894 (UTC).

NEVADA: Elko Co., Humbolt National Forest, near Clover Creek, *Robertson* 300, 19 July 1949 (USFS).

NORTH DAKOTA: Billings Co., Medora, *Stevens* 11, 29 June 1938 (MONT). Dunn Co., R. 92, Twp. 149, *Heidenreich* s.n., 11 June 1936 (NDA).

OKLAHOMA: Cimarron Co., 2 mi. N. of Kenton, *Hess* 723, 26 May 1966 (OKL).

UTAH: Box Elder Co., Wellsville Mts., *Burke* 3012, 23 May 1932 (UTC). Carbon Co., Wellington, *Cottam* 2046, 5 June 1927 (BRY); West Tavaputs Plateau, *Maguire* 18515, 9 June 1940 (UTC, BRY); West side of Schofield Reservoir, *Welsh* 6521, 1 August 1967 (BRY). Davis Co., Mueller Park, *Brizzee* s.n., 28 April 1940 (UT). Garfield Co., Bryce Canyon, *Rollins* 2453, 7 July 1938 (USFS). Grand Co., Arches National Monument, *Welsh* 1903, 2 May 1963 (BRY). Salt Lake Co., Fort Douglas, *Brenchle* s.n., 25 May 1918 (NDA); Parley's Canyon, *Vickery* 657, 24 June 1956 (ARIZ). San Juan Co., Coon Canyon, *Moore* s.n., 4 July 1917 (PH); La Sal Creek, *Cutler* 2652, 9 July 1939 (OKL); So. of Mexican Hat, *Hitchcock* 1345, 27 June 1930 (MONT). Uintah Co., 1 mi. West of Rainbow, *Homgren* 1819, 4 June 1965 (BRY, UTC). Wasatch Co., 12 mi. East of Soldier Summit, *Maguire* 18406, 5 June 1940. Utah Co., Bridal Veil Falls along Provo River, *Pennell* 22570, 5 July 1938 (COLO).

WYOMING: Carbon Co., 8 mi. West of Medicine Bow, *Porter* 4584, 15 June 1948 (COLO). Sublette Co., Pine Grove Ridge, *Cazier* C-124, 23 July 1931 (USFS). Teton Co., 10 mi. South of Jackson, *Rethke* 3894, 2 July 1938 (COLO).

Plants from the Wallowa mountain of Oregon, and southern British Columbia, are intermediate in several characters between ssp. *boreale* and ssp. *mackenzii*, but tend to resemble more closely ssp. *mackenzii*; thus plants which occur in these areas will be referred to on the distribution maps as the ssp. *mackenzii*.

The var. *boreale* is usually assumed to inhabit only the plains regions of Canada, and the lower mountain slopes of the Rockies. But it is also commonly found at elevations of 8000 feet or more in many areas throughout its range. Flowering occurs from early May to early August. 2N=16.

The taxon described by Rollins (1940) as *H. boreale* var. *utahense* is not recognized here as a distinct entity for several reasons. Mass collections from the type locality of the var. *utahense* yield plants which are typical of var. *boreale* and of var. *utahense* as well as intermediates between them. Plants of *H. boreale* in the pinyon-juniper woodlands of southern and eastern Utah have small leaves. These grade with plants which have larger flowers and larger leaves in more moist canyons and slopes in northern portions of the state. There appears to be no chromosomal differences between plants from the two regions.

Hedysarum boreale Nutt. ssp. *boreale* var. *gremiale* (Rollins) Northstrom and Welsh comb. nov. (Fig. 6, E.)

Hedysarum gremiale Rollins, Rhodora, 42:230. 1940.

Distribution: Dry slopes, ravines, and pinyon-juniper communities from 5000-6000 ft. elevation in the Uintah Basin of Utah.

Specimens examined:

UTAH: Uintah Co., Moenkopi Shale, Split Mt. Gorge, Dinosaur Nat. Monument, *Brotherson* 787, 15 July 1956 (BRY); West of Vernal, *Rollins* 1733, 16 June 1937 (PH, OKL Isotype). Duchesne Co., North of Myton, *Pennell* 22497, 1 July 1938 (PH).

This taxon can be distinguished from the other varieties of the ssp. *boreale* only in the fruiting stage. None of the characters discussed in Rollins' paper (1940) other than the spiny fruits can be used to separate this entity from the other members of the complex. Even the possession of spiny fruits is not infallible, because plants with short but distinct spines commonly occur in Wyoming and as far north as Alberta. It appears that this entity is just one extreme in an essentially continuous series grading from the var. *cinerascens*. However, the more abundant development of spines on the fruits of plants from the Uinta Basin indicate that the plants should be treated in some taxonomic rank. Flowering from May to July. 2N=16.

Hedysarum boreale Nutt. ssp. *boreale* var. *cinerascens* (Rydb.) Rollins, Rhodora 42:235. 1940 (Fig. 7).

Hedysarum canescens Nutt., ex. T. & G. Fl. N. Am. 1:357. 1838.

Hedysarum cinerascens Rydb., Mem. N. Y. Bot. Garden. 1:257. 1900.

Hedysarum macquenzii var. *canescens* (Nutt.) Fedtschenko, Acta Hort. Petrop. 19:362. 1902 (sic.).

Hedysarum boreale var. *cinerascens* (Rydb.) Rollins, Rhodora. 42:234. 1940.

Hedysarum boreale var. *obovatum* Rollins, Rhodora. 42:235. 1940.

Hedysarum boreale var. *cinerascens* f. *album* B. Boi., Nat. Canad. 87:34. 1960.

Distribution: Alberta and Saskatchewan, south through Idaho and Montana to Nevada, southern Wyoming and eastern Utah. Dry banks and ravines from 5000 to 8000 feet elevation.

Representative specimens:

ALBERTA: Milk Mts., Boivin 9502, 26 June 1952 (OKL); E. of Waterton River,



Fig. 7. *Hedysarum boreale* ssp. *boreale* var. *cinerascens* A. habit. B. leaflet detail.

Breitung 16486, 23 July 1953 (COLO); Rosedale Trail, *Moodie* 1020, 22 June 1915 (OSC); Elkwater, *Payne* 41, 10 July 1958 (MONT).

IDAHO: Custer Co., W. of Salmon River, *Hitchcock* 8989, 15 June 1944 (MONT, UTC); W. of Clayton, *Hitchcock* 10794, 5 August 1944 (UTC). Jefferson Co., *Moran* s.n., 15 June 1967 (BRY).

MANITOBA: Near Churchill, *Brues* s.n., 6 July 1963 (OKL).

MONTANA: Broadwater Co., 7 mi. E. of Townsend, *Hitchcock* 11824, 1 July 1945 (PH, UTC). Fergus Co., Big Snowy Range, *Bamberg* s.n., 10 July 1958 (COLO); 1 mi. N. of Heath, *Hitchcock* 11929 (UTC, PH, COLO). Gallatin Co., Bear Creek Road, *Wright* s.n., 8 June 1952 (MONT). Glacier Nat. Park, 3 mi. W. of E. Entrance, *Booth* s.n., 14 June 1952 (ARIZ). Lewis and Clark Co., Ear Mt. Ranger Station, *Butler* D 3-12, 1 July 1921 (USFS); Livingston Park Co., 25 mi. N. of Field, *Single*, 17 June 1936 (MONTU). Madison Co., Hammond Creek, *Hitchcock* 16721, 23 July 1947 (UTC); 6 mi. S. of Ennis, *Hitchcock* 16808, 25 July 1947 (COLO, UTC); N. W. limit of Gravelly Range, *Hitchcock* 12541, 19 July 1945 (OSC, MONT). Meager Co., 6 mi. N. W. of White Sulphur Springs, *Hitchcock* 12182, 11 July 1945 (PH, UTC, OSC, MONT).

NEVADA: Elko Co., Thorp Creek, Humboldt Nat. Forest, *Price* 168, 25 July 1928 (USFS).

NORTH DAKOTA: Billings Co., North side of Butte, *Stevens* s.n., 3 August 1923 (NDA). Kidder Co., 8 mi. N. of Lake Williams, *Moir* s.n., 27 July 1956 (NDA). Slope Co., Saddle Butte, *Stevens* s.n., 14 June 1963 (NDA). Ward Co., 2 mi. W. of Minot, *Bare* 1053, 25 June 1968 (NDA). Wells Co., Hurdfield, *Stevens* 696, 27 June 1943 (NDA). Williams Co., Buford, *Stevens* s.n., 21 June 1945 (NDA).

QUEBEC: Riviere Vaureal, *Louis-Marie* 20871, 28 July 1925 (PH).

SASKATCHEWAN: Location unknown, *Boivin* 8796, 11 Aug. 1951 (NDA); Battle Creek Ranger Station, Cypress Hills, *Breitung* 5054, 25 July 1947 (UTC).

UTAH: Summit Co., Elk Horn Ranger Station, *Stewart* 20, 6 June 1921 (USFS); Uintah Co., 2 mi. North of Vernal, *Porter and Rollins* 5673, 26 June 1951 (PH).

WYOMING: Big Horn Co., Big Horn Forest, Dayton-Kane Road, Dickson 250, 17 June 1932 (USFS); Red Bank, *Goodding* 332, 20 July 1901 (MONT, UTC, ARIZ); Dayton, *Stevens* 38-329, 3 July 1938 (NDA). Fremont Co., 10 mi. west of Dubois, *Porter and Rollins* 5780, 27 July 1951 (PH). Natrona Co., Near Pathfinder Reservoir, *Porter* 4506, 4 June 1948 (MONT). Park Co., 20 mi. North of Cody, *Porter* 5442, 11 July 1950 (PH, OKL). Sublette Co., 20 mi. west of Big Piney, *Payson* 2617, 9 July 1922 (PH, OSC). Teton Co., 20 mi. South of Jackson U.S. 187, *Maguire* 12845, 2 August 1935 (UTC); Elk Ranch, east side of Jackson Hole, *Reed* 2315, 13 June 1948 (OKL); Snake River bottom, *Williams* 1339, 24 July 1933 (UTC, OSC).

This taxon represents another extreme of a series grading into var. *boreale*. Its greatest development is expressed in northern and central Montana. Plants from North Dakota, eastern Utah and eastern Idaho are intermediate between var. *boreale* and var. *cinerascens*. Flowering occurs from May to early August. 2N=16.

There are several reasons for reducing the plant described by Rollins (1940) as *H. boreale* var. *obovatum* to synonymy under var. *cinerascens*. The specimen on which var. *obovatum* is based differs in no other characters from var. *cinerascens*, except for the obovate lower leaflets; but obovate leaflets are present to a greater or lesser extent in all the varieties of *H. boreale*. Also, a visit to the type locality of the entity in 1968 has failed to yield anything but plants typical of var. *boreale*. Perhaps var. *obovatum* should be regarded as merely a teratological form of the var. *cinerascens*.

Hedysarum boreale Nutt. ssp. *mackenzii* (Richards.) Welsh, Great Basin Nat. 28:152. 1968. (Fig. 8.)

Hedysarum mackenzii Richards, in Frankl. 1st. Journ. Bot. App. 745. 1823.

Hedysarum americanum var. *mackenzii* Britt., in Mem. Torrey Bot. Club. 5:202. 1894.

Hedysarum mackenzii var. *mackenzii* f. *niveum* B. Boi., Canad. Field-Nat. 65:20. 1951.

Hedysarum boreale var. *mackenzii* (Richards.) C. L. Hitchc., in Vasc. Pl. Pac. N. W. 3:275. 1961.

Stems 1.5-5 dm long, usually unbranched above, stipules pale tan, or white-translucent with brown streaks; flowers 5-20, 15-26 mm long, usually purple, occasionally pink or pale pink; racemes compact, 2-10 cm long; leaflets usually green and glabrous above, grayish-green and pubescent below; articles 3-8, margins of articles and reticulations often black pigmented.

Distribution: Alaska to Newfoundland, south of northeast Oregon, and east through southern British Columbia, to Quebec, and also in eastern Siberia.

Representative specimens:

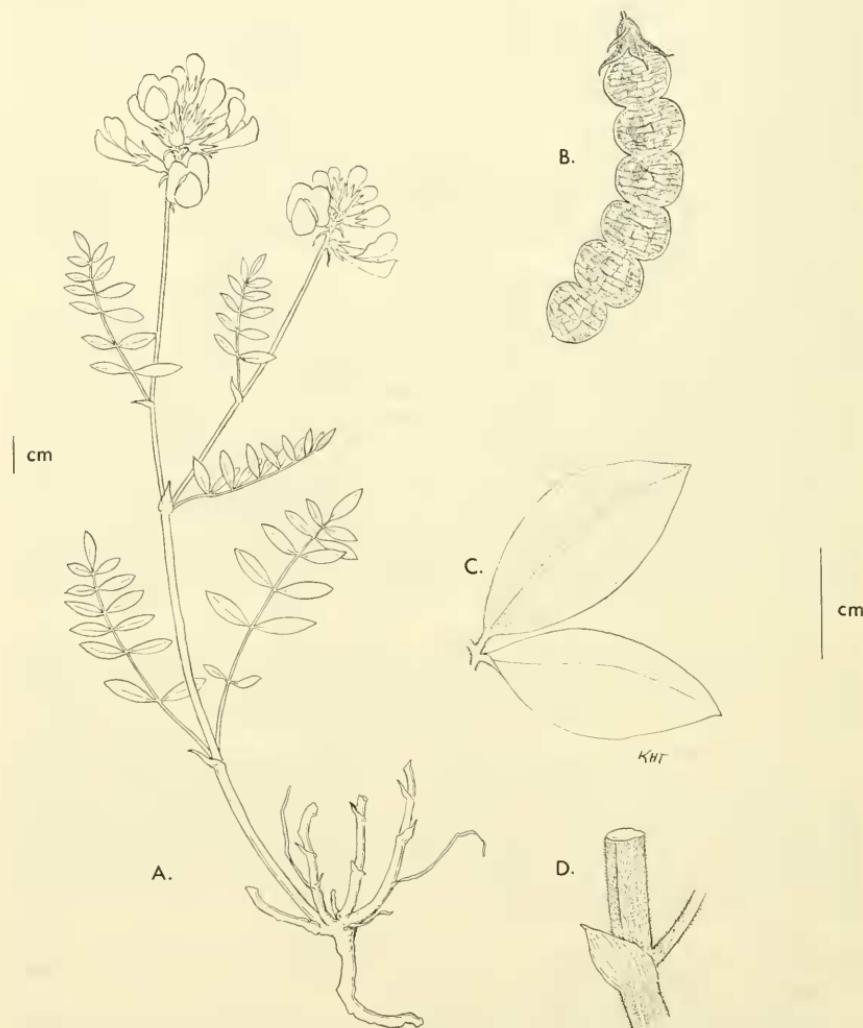


Fig. 8 *Hedysarum boreale* ssp. *mackenzii*. A. habit sketch. B. loment. C. leaflet detail. D. stipule detail.

ALASKA: Bering Strait District, *Viereck* 4409, 13 July 1960 (COLO); Mile 225 Richardson Highway, *Welsh* 5041, 2 August 1965 (BRY); Mount McKinley National Park, *Welsh* 4834, 21 July 1965 (BRY); Mile 217.3 Richardson Highway, *Williams* 1273, 22 July 1965 (OSC, BRY).

ALBERTA: Vicinity of Banff, *Brown* 75, 8 June 1906 (PH); Jasper National Park, *Davis* 5082, 22 July 1962 (BRY); North Fork Belly River, *Shaw* 343, 4 July 1967 (BRY); Mt. Castleguard, *Strock* s.n. 29 August 1930 (UTC, PH); South of Peyto Lake, *Weber* 2429, 12 July 1941 (COLO).

BRITISH COLUMBIA: Vicinity of Field, *Brown* 538, 16 July 1906 (PH); North end of Azouzetta Lake, *Calder* 14022, 4 August 1954 (OSC); 16 miles south of Lillooet, *Calder* 17572, 18 June 1959 (OSC); Halfway River, *Henry* 9, 4 July 1931 (PH); Summit Lake, *Welsh* 5447, 22 June 1966 (BRY).

MANITOBA: Churchill, *Cope* s.n., 10 July 1934 (PH); Fort Churchill, *Gillett* 1913, 30 June 1948 (OKL); Limestone river banks near Gillam, *Shofield* 1099, 12 July 1950 (COLO).

NORTHWEST TERRITORIES: Opposite Fort Simpson, *Cody* 8466, 30 June 1955 (ARIZ); Moraine Point, Great Slave Lake, *Lewis* 479, 30 June 1951 (COLO, OKL); Franklin Expedition, Collector unknown (PH, Isotype); Cambridge Bay, *Stephens* 1004, 10 July 1962 (OKL).

OREGON: Union Co., half mile north of east Eagle Creek Falls, *Head* 1045, 30 June 1957 (OSC). Wallowa Co., Wallowa Mts., *Cusick* 3694, 9 August 1911 (OSC); Hurricane Creek, *Head* 127, 29 July 1951 (BRY); Hurricane Creek Forest Camp, *Maguire* 26687, 19 July 1946 (COLO, UTC, ARIZ); Hurricane Creek trail about a half mile south of Falls Creek, *Mason* 5718, 26 August 1962 (OSC); Border of Ice Lake, *Mason* 6461, 8 August 1963 (OSC); Wallowa Forest, *Reid* 738, 27 July 1938 (USFS).

QUEBEC: Ungava Bay, *Bonde* 283, 27 July 1948 (COLO).

SASKATCHEWAN: Near Bear Creek, *Brown* 909, 14 June 1908 (PH).

YUKON TERRITORY: Mile 1019, Alaska highway, *Welsh* 4056, 9 June 1965 (BRY); Mile 114.7 Dawson highway, *Welsh* 5560, 25 June 1966 (BRY).

H. mackenzii is essentially restricted to rocky slopes, roadsides, gravel bars, sandy places and other areas which are in early stages of succession. The plants occasionally occur in tundra and open woodlands. Flowering takes place from early June to August. 2N=16.

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